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## FORAGING BEHAVIOUR OF MEGACHILID BEES ON *SWAINSONA CANESCENS* (FABACEAE) AND ITS COEVOLUTIONARY IMPLICATIONS

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### ABSTRACT

Females of the Megachilid bee *Chalicodoma semiluctuosa* were observed foraging on the vertical inflorescences of *Swainsona canescens* on Cooloomia Nature Reserve 70 km north of Kalbarri in Western Australia. The bees tended to start foraging on each inflorescence below the uppermost flowers, they moved upwards between flowers more frequently than downwards, and they missed a lot of open flowers on each inflorescence. These behavioural patterns concur with those adopted by North American bumblebees feeding on plants with vertical inflorescences. Further work may show that *S. canescens* possesses a number of floral characteristics that have coevolved with the foraging behaviours of its Megachilid pollinators to reduce pollen wastage, to maximize outcrossing in environmentally unfavourable years and to increase self-pollination in favourable years.

### INTRODUCTION

Interest in the foraging behaviour of bees and coevolved features of their plants was recently stimulated by Pyke (1978). He studied the behaviour of three North American bumblebees (*Bombus* spp.) that fed on the nectar of five plant species all characterized by flowers on vertical inflorescences (*Delphinium nelsoni*, *D. barbeyi*, *Aconitum columbianum*, *Epilobium angustifolium* and *Penstemon strictus*). Pyke found that the bumblebees consistently commenced foraging at the bottom of inflorescences, they tended to move vertically up each inflorescence, they tended to leave each inflorescence before reaching the top and they missed flowers as they moved upwards. In four of the five plants studied, nectar abundance per flower decreased with flower height on an inflorescence, flowers with receptive stigmas were restricted to the bottoms of the inflorescences while flowers shedding pollen occurred above them, and flowers were arranged approximately in spirals on the inflorescences. Pyke proposed that these



Fig. 1.—Photographs of (top) a *Chalicodoma semiluctuosa* taking nectar from the uppermost open flower on an inflorescence of *Swainsona canescens*, and (bottom) ventral view of a *Chalicodoma semiluctuosa* showing substantial amounts of *Swainsona canescens* pollen adhering to the undersurface of the abdomen (without pollen this surface is normally black). Scale in the top photograph is 5 mm, scale in the bottom photograph is 2 mm.

features of the plants and the foraging behaviours of their bumblebee pollinators represented coevolved adaptations. Because of the pattern of nectar abundance within inflorescences, bumblebees maximised their net rate of energy gain by foraging in the manner observed. At the same time, the plants benefitted from the bumblebees' behaviour because outcrossing was promoted and wastage of pollen was minimized.

It is of interest to consider whether a similar situation applies in bee-pollinated plants with vertical inflorescences in the Australian flora. *Swainsona canescens* (Fabaceae), an annual herbaceous species of the central and western Australian arid zone, provides a suitable medium for such a study. Under favourable conditions, mature plants produce 100+ vertical inflorescences up to 50cm high, each of which has 10-15 spirally arranged open flowers at any given time when in full bloom.

During September 1979, I encountered large populations of *Swainsona canescens* on Cooloomia Nature Reserve (No. 36127) of 50,000 hectares, located between Shark Bay and the lower Murchison River near the central western coast of Western Australia. At one population selected for detailed investigation (25km S.W. of Cooloomia homestead, 27°08'S, 114°08'E) each plant was being visited by 3-5 females of the fast-flying Megachilid bee *Chalicodoma semiluctuosa* (Fig. 1) and an occasional individual of a smaller indeterminate *Chalicodoma* species at any given time throughout the day. Aspects of the foraging behaviour of *C. semiluctuosa* were observed and quantified to ascertain whether behaviours obtained comparable to those reported by Pyke (1978).

## OBSERVATIONS AND DISCUSSION

It was found that the females of *Chalicodoma semiluctuosa* tended to start feeding below the uppermost flowers on inflorescences (79% of 41 observations), that 69% of interflower movements within inflorescences were up and 31% were down (N=78), and that the mean  $\pm$  S.E. number of flowers visited per inflorescence was  $2.9 \pm 0.3$  (N=41), considerably less than the 10-15 open flowers available per inflorescence. These data in general concur with the observations of Pyke (1978) on foraging behaviour of *Bombus* spp., although *Chalicodoma semiluctuosa* started feeding at the top of inflorescences and moved downwards between flowers more frequently than did the North American bumblebees. Such slight discrepancies may be related to the fact that *C. semiluctuosa* was gathering pollen as well as nectar (Fig. 1) whereas Pyke's bumblebees were only harvesting nectar.

The clear trends shown by *C. semiluctuosa* towards starting on each inflorescence below the uppermost flowers, moving upwards between flowers more frequently than downwards, and missing a lot of open flowers on each inflorescence suggest that *Swainsona canescens* may exhibit similar characteristics to the plant species studied by Pyke (1978), namely decreasing nectar abundance as the inflorescence is ascended, protandry (meaning that older flowers with receptive stigmas occur at the bottom of inflorescences whereas younger flowers with unreceptive stigmas that are shedding pollen occur towards the top), and self-compatibility. If future research confirms that *S. canescens* has these characteristics, then a strong case for coevolution of this species and its Megachilid pollinators could be made along the lines of those proposed by Pyke (1978).

Another aspect of the pollination ecology of *S. canescens* warranting further study concerns the relationships between plant size, environmental conditions, the breeding system and pollinator foraging movements. The Western Australian study site visited in 1979 had enjoyed good rainfall prior to September and contained very large plants (averaging 1m+ in diameter and with 100+ inflorescences). In contrast, much smaller individuals with only 1-10 inflorescences per plant were observed in drier, less favourable sites in the Shark Bay — Murchison River area. It was found that females of *Chalicodoma semiluctuosa* confined a large proportion of their movements between flowers within plants rather than between plants at the study site. In so doing, they may have effected predominant self-pollination on the large, many-flowered plants



of *Swainsona canescens*. Presumably, bees foraging on small, few-flowered plants in less favourable sites would move between plants more often and thus effect a relatively high level of cross-pollination. Thus, due to the behavioural patterns of the bee pollinators, the growth of plants in response to seasonal influences may lead to enhanced outcrossing in unfavourable years and to increased levels of self-pollination in favourable years. An investigation of this hypothesis would provide valuable insights into the reproductive strategies adopted by *S. canescens* and related species in coping with the environmental vicissitudes of the Australian arid zone.

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### SOME VERTEBRATES RECORDED ON A VISIT TO QUEEN VICTORIA SPRING IN DECEMBER 1977

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Queen Victoria Spring is located 70 kilometres north of Zanthus, a siding on the Transcontinental Railway. A general description and history of the area has been documented by Slater and Lindgren (1955) and Burbidge *et al.* (1976). From November 30 to December 13, 1977, three members of the Zoology Department, University of Western Australia, camped 2.5 kilometres south of the spring. During this visit the average maximum temperature was 39.2° C and the average minimum 15.0° C. The humidity varied between 34% and 86%. Some light rain fell on November 30 and December 12 but sufficient to only form 1 or 2 pools of water in the claypan adjacent to the spring. The spring itself (more correctly a soak) was dug out to a depth of 1.8 metres but no water was found, only damp sand. There was no evidence that the spring had been used recently as a network of spider webs covered the spring depression.

The following is an annotated list of the mammals, frogs and reptiles recorded during this visit. An extensive bird list for the area has been compiled by Serventy (1956) and Slater and Lindgren (1955). All specimens collected during this visit were lodged with the Western Australian Museum and accession numbers are quoted.

#### MAMMALS

Western Grey Kangaroo (*Macropus fuliginosus*) Commonly sighted in the sand dune area to the east of the spring and in the vicinity of the campsite (mallee/spinifex). One found dead on the track 0.5 kilometres south of the spring.

Euro (*Macropus robustus*) One seen near the south boundary of the Queen Victoria Spring Wildlife Sanctuary. Several seen near granite outcrops between 5 mile and 12 mile rockholes, north-west of Cundeelee Mission.

Ride's Ningau (*Ningau ridei*) One male (5.5 grams, M15986) trapped in *Callitris/Eucalypt* 0.5 kilometres south of the spring.

Troughton's Dunnart (*Sminthopsis ooldea*) One female (6.0 grams, M15895) trapped in Mallee/Spinifex 2.5 kilometres south of the spring.

The following bat species were shot at night on the side of the claypan at Queen Victoria Spring.

Little Flat Bat (*Tadarida planiceps*) — male 9.0 grams, M18475.